The faunistic diversity of cave-dwelling spiders (Arachnida, Araneae) of Greece

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doi: 10.5431/aramit4004

Abstract: Until today, from Greek caves a total of 109 species of spiders belonging to 25 families are known. One species, the linyphiid *Porrhomma convexum* (Westring, 1861) was recorded here for the first time in Greece. The 109 species are distributed in caves of different geographic territories as follows: Thrace – 8 species, Macedonia – 18, Epirus – 1, Thessaly – 6, Central Greece – 3, Attiki-Saronic Islands – 24, Peloponnese – 15, Evoia-Vories Sporades – 1, Eastern Aegean Islands – 5, Cyclades – 3, Dodecanese – 6, Ionian Islands – 23, Crete – 47. The largest fraction of troglobite species were encountered mainly in the territories of Crete – 15 species (5 of which are anophthalmic), the Ionian Islands – 4, Thrace – 2 (both anophthalmic), the Attiki-Saronic Islands – 2 (both anophthalmic), the Peloponnese – 2 (one anophthalmic), and Macedonia, Thessaly, and the Cyclades – each with 2 species. The richness of the troglobitic spiders in these regions strengthens the assumption that they were major centres of speciation and evolution for the species of this group. According to their current distribution, the established 109 species can be classified into 12 zoogeograpical categories, grouped into 4 complexes (widely distributed, European, Mediterranean, endemics). The largest number of species belong to the endemic complex (53.2 %) and are also the most characteristic and reflect the local character of the cave-dwelling spiders.

Key words: cave-spiders fauna, endemics, troglobites, zoogeography

The earliest data on Greek cave-dwelling spiders were presented by SIMON (1885), KULCZYŃSKI (1903), ROEWER (1928, 1959), DRENSKY (1936); KRATOCHVÍL (1937, 1938), HADJISSARANTOS (1940), and FAGE (1945). More recent publications derive from the investigations of BRIGNOLI (1968, 1971a, 1971b, 1972, 1974a, 1974b, 1974c, 1976, 1977, 1978, 1979, 1984), DEELEMAN-REINHOLD (1971, 1977, 1983, 1985, 1989, 1993), DEELEMAN-REINHOLD & DEELEMAN (1988), SENGLET (1971, 2001), DELTSHEV (1979, 1985, 1999, 2000, 2008), BERON (1985, 1986), BERON & STOEV (2004), THALER & KNOFLACH (1995), WUNDERLICH (1995), BOSSELAERS (1998), BOSSELAERS & HENDERICKX (2002), GASPARO (2003, 2004a, 2004b, 2005a, 2005b, 2006, 2007, 2008, 2009), CHATZAKI et al 2002, BOSMANS & CHATZAKI (2005), CHATZAKI & ARNEDO (2006), and PLATNICK (2009). The critical incorporation of all available literature records and the accumulation of new data are now sufficient to allow a critical analysis of the distribution of spiders established in the caves of Greece.

Study area and material

Greece is a country in south-eastern Europe, situated on the southern end of the Balkan Peninsula. The country has borders with Albania, the Republic of Macedonia and Bulgaria to the north, and Turkey to the east. The Aegean Sea lies to the east and south of mainland Greece, while the Ionian Sea lies to the west. Both parts of the Eastern Mediterranean basin feature a vast number of islands, islets and rock islands (Fig.1). Two-thirds of the territory of Greece is dominated by limestone, many of which are karstified (CLENDENON 2009).

The territory of Greece can be divided into 13 geographical regions (BOSMANS & CHATZAKI 2005; Fig. 1). There are 7 geographical regions on the mainland: Thrace, Macedonia, Epirus, Thessaly, Central Greece, Attica and the Peloponnese. The Ionian Islands are situated on the western border of Greece in the Ionian Sea. There are several island groups in the Aegean Sea on the eastern side of Greece: Evoia and the Sporades, the Saronic Islands (grouped with Attica), the Cyclades, the Eastern Aegean Islands, the Dodecanese and Crete (Fig. 1).

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submitted: 30.12.2010, accepted: 9.4.2010; online: 10.1.2011

Results

Species composition

The spiders established in the caves of Greece (Mainland and Insular part) are represented by 109 species, included in 52 genera and 25 families: Ctenizidae – 1, Filistatidae – 1, Sicariidae – 1, Scytodidae – 1, Leptonetidae – 9, Pholcidae – 10, Segestriidae – 3, Dysderidae – 12, Oonopidae – 1, Mimetidae – 1, Ere-

Figure 1: Map of different geographical regions in Greece.

sidae – 1, Uloboridae – 1, Nesticidae – 4, Theridiidae – 4, Anapidae – 1, Linyphiidae – 16, Tetragnathidae – 4, Araneidae – 1, Lycosidae – 1, Agelenidae – 21, Amaurobiidae – 4, Gnaphosidae – 6, Philodromidae – 1, Thomisidae – 2, Salticidae – 2 (Table 1). One species is new for the Greek spider fauna: *Porrhomma convexum* (Westring, 1861) (marked in the list with *), a spider with a Holarctic distribution and widespread in European caves. It is also well represented in the caves of the Balkan Penisula – and not only established in the caves of Croatia, Romania and Turkey (DELTSHEV 2008). The number of species is high and represents about 13 % of the Greek spiders. This is also evident from a comparison with the number of cave-dwelling spiders recorded from the other countries of the Balkan Peninsula: Bulgaria – 99, Croatia – 63, Serbia – 59, Bosnia and Herzegovina – 52, Macedonia – 44, Montenegro – 44, Slovenia – 43, Albania – 10, Turkey – 8, and Romania – 4 (DELTSHEV 2008). The established number of species, however, depends not only on the size of the regions, but also on the degree of exploration. The most characteristic are the families: Leptonetidae (8.2 %), Pholcidae (9.2 %), Dysderidae (11 %), Linyphiidae (14.6 %), and Agelenidae (19.2 %). The families with largest number of anophthalmic species are Leptonetidae (6), Dysderidae (3), Nesticidae (2), and Linyphiidae (1). The genera with the largest number of species are *Tegenaria* (8), *Lepthyphantes* (6), *Harpactea* (5), and *Histopona* (5).

The species are distributed in caves belonging to the geographic territories of Greece as follows: Thrace – 8 species, Macedonia – 18, Epirus – 1, Thessaly – 6, Central Greece – 3, te Attiki-Saronic Islands – 24, the Peloponnese – 15, Evoia-Voroies Sporades – 1, the Eastern Aegean Islands – 5, the Cyclades – 7, the Dodecanese – 6, the Ionian Islands – 23, Crete – 47 (Table 1). We also have to emphasise that the degree of exploration in these territories is not equal: the territories of Evoia-Sporades, the Cyclades, the Dodecanese and Central Greece are less explored.

Cave-dwelling spiders can be categorised into four ecological groups (SKET 2008):

- troglobites: species limited to a life cycle in caves. Often they show a suite of characters, associated with their adaptation to subterranean life: loss of pigment, loss of eyes and elongation of appendages.
- eutroglophiles: species which can live their entire life in caves, but also occur in other environments.
- subtroglophiles: species which utilise caves, but must leave the caves to complete their life cycle.
- trogloxenes: species which occur underground sporadically.

The largest fraction of troglobite species was encountered mainly in the caves of the territories of Crete –15 (5 anophthalmic), the Ionian Islands – 4, Thrace – 2 (2 anophthalmic), the Attiki-Saronic Islands 2 (2 anophthalmic), the Peloponnese – 2 (1 anophthalmic), and Macedonia, Thessaly and the Cyclades each by 2 species (Table 1). All troglobites are endemics for the territory of Greece or the Balkan Peninsula.

Very important is the presence of eutroglophiles (35 species), because together with troglobites (29 species), they can be considered as dependent faunistic elements of caves. The largest number of species is established in the caves of Crete (14 species), the Ionian Islands (11 species), the Attiki-Saronic Islands (9 species), Macedonia (8 species), and the Peloponnese (8 species). Here, the endemics are represented by 14 species (35 %). A present day example of active subterranean colonisation and cave penetration are the species *Lepthyphantes centromeroides* and *Palliduphantes spelaeorum*, widespread in the Balkan Peninsula (DEELEMAN-REINHOLD 1978). Here, the species *Palliduphantes istrianus* should also be included.

Table 1: Species composition of cave dwelling spiders in Greece

Category (CAT): tb – troglobite; **tba** – troglobite anophtalmic; **etph** – eutroglophile; **stph –** subtroglophile; **tx -** trogloxene

Zoogeography (Z_G): COS – Cosmopolitan; **H –** Holarctic; **P** - Palearctic; **WP** - West Palearctic; **ECA** - European-Central Asian; **E** - European; **MSEE** - Middle Southeast European; **MCA** – Mediterranean-Central Asian; **M** - Mediterranean; **NM** - North Mediterranean; **NEM** - Northeast Mediterranean; **E –** Endemics; **ETHR -** Endemic for Thrace; **EMTH -** Endemic for Macedonia and Thrace; **EEP** - Endemic for Epirus; **EETI** - Endemic for Epirus, Thessaly and Ionian Islands; **ECGR -** Endemic for Central Greece; **EAS -** Endemic for Attiki-Saronic Islands; **ECOG –** Endemic for continental Greece**; EPE -** Endemic for Peloponese; **EAP** - Endemic for Attiki-Saronic Islands and Peloponese; **EPI –** Endemic for Peloponnisus and Ionian Islands; **EEAI -** Endemic for Eastern Aegean Islands; **ECY -** Endemic for Cyclades; **EKA -** Endemic for Karpathos; **EIO -** Endemic for Ionian Islands; **ECR –** Endemic for Crete; **EGR** - Endemic for continental and island Greece; **EBP -** Endemic for Balkan Peninsula.

Distribution: THR – Thrace**; MA –** Macedonia; **EP –** Epirus; **THE –** Thessaly; **CGR –** Central Greece; **ASI -** Attiki-Saronic Islands; **PE –** Peloponnese; **ESI -** Evia-Sporades; **EAI -** Eastern Aegean Islands; **CY -** Cyclades; **DO –** Dodecanese**; IO –** Ionian Islands; **CR –** Crete.

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Cyrtaucheniidae															
Cyrtocarenum grajum (C.L. Koch 1836)	tx	ECR													x
Filistatidae															
Filistata insidiatrix (Forsskål, 1775)	stph	M		x										x	x
Sicaridae															
Loxosceles rufescens (Dufour, 1820)	stph	COS		x				x	x				x		x
Scytododae															
Scytodes thoracica Latreille, 1804	stph	H							x				x	x	x
Leptonetidae															
Barusia laconica (Brignoli, 1974)	tb	EPE							x					x	
Cataleptoneta sengleti (Brignoli, 1974)	tba	ECR													x
Leptonetela andreevi Deltshev, 1985	tba	ECY													
Leptonetela kanellisi (Deeleman-Reinhold, 1971)	tba	EAS						x							
Leptonetela strinatii (Brignoli, 1976)	tba	EAS						x							
Leptonetela thracia Gasparo, 2005	tba	ETHR	x												
Sulcia cretica cretica Fage, 1945	tb	ECR													x
Sulcia cretica lindbergi Dresco, 1962	tba	EEP			x										x
Sulcia cretica violacea Brignoli, 1974	tb	EETI			x	x								x	
Pholcidae															
Holocnemus pluchei (Scopoli, 1763)	etph	M		x				x					x	x	x
Hoplopholcus figulus Brignoli, 1971	etph	EEAI									x				
Hoplopholcus labyrinthi (Kulczyński, 1903)	tb	ECR													x
Hoplopholcus minotaurinus Senglet, 1971	tb	ECR													x
Hoplopholcus minous Senglet, 1971	stph	EKA											x		
Pholcus creticus Senglet, 1971	etph	ECR													x

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Pholcus opilionoides (Schrank, 1781)	etph	H													x
Pholcus phalangioides (Fuesslin, 1775)	etph	COS		x								x			x
Spermophora senoculata (Dugès, 1836)	etph	H											x		
Stygopholcus photophilus (Senglet, 1971)	etph	EGR		x		x					x			x	x
Segestridae															
Segestria florentina (Rossi, 1790)	tx	WP						x							x
Segestria sbordonii Brignoli, 1984	tx	ECR													x
Segestria senoculata (Linnaeus, 1758)	tx	P												x	
Dysderidae															
Dysdera cephalonica Deeleman-Reinhold, 1988	tx	EIO											x		
Dysdera crocata C.L. Koch, 1838	etph	COS													x
Dysderocrates gasparoi Deeleman-Reinhold, 1988	etph	EIO												x	
Dysderocrates marani (Kratochvíl, 1937)	etph	ECR													x
Harpactea catholica (Brignoli, 1984)	etph	ECR													x
Harpactea corinthia Brignoli, 1984	etph	EPE							x						
Harpactea loebli Brignoli, 1974	tx	EIO												x	
Harpactea rubicunda (C.L. Koch, 1838)	stph	E	x	x											
Harpactea strinatii Brignoli, 1979	tba	EPE							x						
Minotauria attemsi Kulczyński, 1903	tb	ECR													x
Minotauria fagei (Kratochvíl, 1970)	tba	ECR													x
Rhodera hypogea Deeleman-Reinhold, 1989	tba	ECR													x
Oonopidae															
Oonops mahnerti Brignoli, 1974	tx	EPE							x						
Mimetidae															
Ero flammeola Simon, 1881	tx	M												x	
Eresidae															
Eresus kollari Rossi, 1846	tx	ECA						x	x						
Uloboridae															
Uloborus plumipes Lucas, 1846	tx	COS						x					x		
Nesticidae															
Nesticus beshkovi Deltshev, 1979	tba	ECR													x
Nesticus cellulanus (Clerck, 1757)	etph	H		x											
Nesticus eremita Simon, 1879	tb	NEM				x				x				x	
Nesticus henderickxi Bosselaers, 1998	tba	K													x
Theridiidae															
Crustulina scabripes Simon, 1881	tx	M											x		
Steatoda castanea (Clerck, 1757)	tx	P													x

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Steatoda grossa (C.L. Koch, 1838)	stph	COS												x	x
Steatoda triangulosa (Walckenaer, 1802)	stph	COS							x						
Anapidae															
Zangherella apuliae (Caporiacco, 1949)	tb	NM												x	
Linyphiidae															
Centromerus milleri Deltshev, 1974	tba	EMTH	x												
Diplocephalus turcicus Brignoli, 1972	tx	NEM						x							
Icariella hauseri Brignoli, 1979	tx	EGR									x				
Lepthyphantes beroni Deltshev, 1979	tb	ECR										x			x
Lepthyphantes beshkovi Deltshev, 1979	tb	ECR													x
Lepthyphantes brignolianus Deltshev, 1979	tb	ECR													x
Lepthyphantes kratochvili Fage, 1945	tb	ECR													x
Lepthyphantes magnesiae Brignoli, 1979	etph	ECOG							x						
Palliduphantes byzantinus (Fage, 1931)	etph	EBP							x						
Palliduphantes epaminondae (Brignoli, 1979)	tb	ECGR					x								
Palliduphantes istrianus (Kulczyński, 1914)	tb	EBP		x										x	
Palliduphantes spelaeorum (Kulczyński, 1914)	tb	EBP		x											
Porrhomma convexum (Westring, 1851)	tb	P		x											
Savignia naniplopi Bosselaers & Henderickx, 2002	tx	ECR													x
Tenuiphantes tenuis (Blackwall, 1852)	tx	E												x	
Tetragnathidae															
Meta bourneti Simon, 1922	etph	WP	x					x	x						
Meta menardi (Latreille, 1804)	etph	E				x		x	x						
Metellina merianae (Scopoli, 1763)	etph	E		x				x						x	x
Tetragnatha montana Simon, 1874	tx	P		x											
Araneidae															
Larinioides suspicax (O.P.-Cambridge, 1876)	tx	E													x
Lycosidae															
Alopecosa albofasciata (Brullé, 1832)	tx	M		x				x							x
Agelenidae															
Allagelena gracilens (C.L. Koch, 1841)	tx	WP						x							
Histopona hauseri Brignoli, 1972	etph	EIO												x	
Histopona isolata Deeleman-Reinhold, 1983	tb	ECR													x
Histopona myops (Simon, 1885)	etph	ECOG				x			x						
Histopona strinatii (Brignoli, 1976)	etph	EP							x						
Histopona thaleri Gasparo, 2005	etph	ECGR					x								
Maimuna cretica (Kulczyński, 1903)	stph	EK													x

TAXA	CAT	Z_G	THR	MA	EP	THE	CGR	ASI	PE	ESI	EAI	CY	DO	IO	CR
Maimuna vestita (C.L. Koch, 1841)	stph	NEM		x				x							
Malthonica dalmatica (Kulczyński, 1906)	etph	NEM									x			x	x
Malthonica ferruginea (Panzer, 1804)	etph	E	x	x				x							x
Malthonica pagana (C.L. Koch, 1840)	etph	MCA						x				x			x
Tegenaria silvestris (L. Koch, 1872)	etph	E						x							
Tegenaria achaea Brignoli, 1977	etph	EEAI									x				
Tegenaria ariadnae Brignoli, 1984	etph	ECR													x
Tegenaria domestica (Clerck, 1757)	etph	COS		x				x	x					x	
Tegenaria hauseri Brignoli, 1979	etph	EIO												x	
Tegenaria labyrinthi Brignoli, 1984	stph	ECR													x
Tegenaria paragamiani Deltshev, 2008	etph	ETHR													
Tegenaria parietina (Fourcroy, 1785)	etph	WP						x				x		x	x
Tegenaria pieperi Brignoli, 1979	tb	ECR													x
Tegenaria schmalfussi Brignoli, 1976	tb	ECR													x
Amaurobiidae															
Amaurobius cretaensis Wunderlich, 1995	tx	ECR													x
Amaurobius deelemanae Thaler & Knoflach, 1995	tx	ECDC										x			
Amaurobius pelops Thaler & Knoflach, 1991	tx	EAP						x							
Amaurobius strandi Charitonov, 1937	tx	SEE						x							
Gnaphosidae															
Drassodes lapidosus (Walckenaer, 1802)	tx	P						x							x
Nomisia ripariensis (Thorell, 1871)	tx	NEM													x
Pterotricha lentiginosa (C.L. Koch, 1837)	tx	NEM						x							x
Zelotes clivicola (L. Koch, 1870)	tx	P						x							
Zelotes femellus (L. Koch, 1866)	tx	NEM		x											
Zelotes oblongus (C.L. Koch, 1833)	tx	MSEE													x
Sparassidae															
Eusparassus walckenaeri (Audouin, 1826)	tx	NEM													x
Philodromidae															
Philodromus collinus C.L. Koch, 1835	tx	E						x							
Thomisidae															
Synema globosum (Fabricius, 1775)	tx	P						x							
Xysticus kochi Thorell, 1872	tx	WP													x
Salticidae															
Evarcha falcata (Clerck, 1757)	tx	P	x												x
Mendoza canestrinii (Ninni, 1868)	tx	P		x											

Table 2: Zoogeographical composition of cave dwelling spiders in Greece

Complexes	Chorotypes		Species	
	Classification	Code	Number	%
Widely distributed	Cosmopolitian	COS	7	6.4
	Holarctic	HOL	5	4.6
	Palearctic	PAL	9	8.2
	West Palearctic	WP	5	4.6
	European-Central Asiatic	ECA	1	0.9
	Total		**27**	**24.7**
European	European	E	8	7.3
	Middle-Southeast European	MSEE	1	0.9
	South East European	SEE	1	0.9
	Total		**10**	**9.2**
Mediterranean	Mediterranean-Central Asiatic	MCA	1	0.9
	Mediterranean	M	5	4.62
	North East Mediteranean	NEM	8	7.3
	Total		**14**	**12.8**
Endemics	Endemic for continental and island Greece	EGR	55	50.4
	Endemic for Balkan Penisnula	EBP	3	2.7
	Total		**58**	**53.2**

The group of subtroglophiles comprises 11 species occurring in dark places such as buildings, screes, rock crevices and caves. They can be considered as regular inhabitants of the caves. Three species are endemics (*Maimuna cretica*, *Hoplppholcus minous*, and *Tegenaria labyrinthi*).

The trogloxenes are represented by 36 species. They are not truly cavernicolous faunistic elements, but their presence in caves should not be ignored. On the other hand some of them will probably be considered subtroglophiles and even eutroglophiles once more information on their ecology is gathered. Here, the endemics are represented by 11 species.

Zoogeographical analysis

According to their current distribution, the established 109 species can be classified into 12 zoogeograpical categories, grouped into four complexes (widely distributed, European, Mediterranean, endemics) (Tab. 1 & 2, Fig. 2).

Best represented is the complex of endemics with 58 species (53.2 %), which include 29 troglobites, 16 troglophiles, and 12 trogloxenes. The established number is high and reflects the local character of the cave fauna. The endemics are best represented in Crete – 26 species and 2 genera (*Minotauria, Rhodera*), the Ionian Islands – 9 species, the Peloponnese – 8 species, Macedonia and the Eastern Aegean Islands – each with 4 species. The recent cave spider fauna is formed after gradual changes in the fauna of the ancient humid Tertiary forests (DEELEMAN-REINHOLD 1977). However, due to a lack of data, it is difficult to determine with certainty which cave spider endemics of the Balkans are Tertiary, and which are Quaternary, elements.

The complex of widely distributed species comprises 36 species (29.2 %). Palearctic species are dominant (47.2 %), followed by Cosmopolitan (19.4 %) Holarctic (13.8 %), West Palearctic (13.8 %), and European-Central Asiatic (5.5 %). The complex includes mostly widespread species associated with lowlands, buildings, caves, woodlands and high altitude zones of mountains. Here characteristic for caves are *Nesticus cellulanus*, *Porrhomma convexum* and *Tegenaria domestica*. These species are also largely

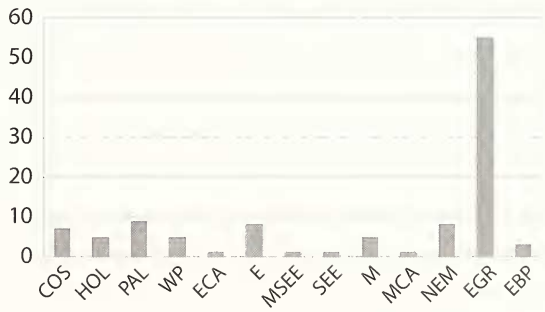

Figure 2: Relative representation of the zoogeographical categories of cave dwelling spiders in Greece (for abbreviations see Table 1).

widespread taxa in European caves where *Porrhomma convexum* occurs in the deep parts.

The European complex includes 10 species (9.2 %). European species are dominant (8 %) among this complex. The Middle Southeast European and Southeast European species are represented by single species - trogloxenes. The complex comprises widespread spiders in Europe and the Balkan Peninsula which inhabit both lowlands and mountains. The most characteristic are *Meta menardi* and *Metellina merianae*, both widespread in European caves.

The Mediterranean complex includes 14 species (12.8 %). The real representation of this category is probably higher because part of the endemic fauna has a Mediterranean origin. Dominant here are the species widespread in the Mediterranean region or part of it, but the real cavernicolous elements are *Nesticus eremita* and *Zangherella apuliae* (characteristic mainly for the superficial underground compartment) distributed in the caves of the north-west part of Greece.

Conclusions

- The faunistic diversity of the reported 109 cave-dwelling spiders shows that Greek caves are characterised by a considerable species richness. This is also supported by comparing the number of cave-dwelling spiders recorded from other countries in the Balkan Peninsula: Bulgaria – 99, Croatia – 63, Serbia – 59, Bosnia and Herzegovina – 52, Macedonia – 44, Montenegro – 44, Slovenia – 43, Albania – 10, Turkey – 8, and Romania – 4 (DELTSHEV 2008).
- The uneven species richness in the caves of different regions of Greece is probably due mainly to the different degree of exploration by researchers.
- Isolation and resulting endemism seems to be the driving force for the cave faunal patterns observed.
- Most characteristic, in a faunal and zoogeographical respect, is the presence of 58 endemic species in Greek caves.
- The high percentage of the endemics (53.2 %) suggests a local speciation process with consequent formation of neo-endemics.
- All troglobitic spiders are endemic, which leads to the conclusion that the regions where they are currently distributed were major centres of speciation.

Acknowledgements

We are especially grateful to our colleagues P. Beron, F. Gasparo, S. Lazarov, M. Naumova, K. Paragamian, B. Pertrov, and P. Stoev for the collected material and valuable discussions. The research was also supported by the Project – Nos. B-1523/05 and BG051PO001-3.3.04/41.

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